

LETTER

Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits

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Abstract

Correlations between community-weighted mean (CWM) traits and environmental gradients are often assumed to quantify the adaptive value of traits. We tested this assumption by comparing these correlations with models of survival probability using 46 perennial species from long-term permanent plots in pine forests of Arizona. Survival was modelled as a function of trait × environment interactions, plant size, climatic variation and neighbourhood competition. The effect of traits on survival depended on the environmental conditions, but the two statistical approaches were inconsistent. For example, CWM-specific leaf area (SLA) and soil fertility were uncorrelated. However, survival was highest for species with low SLA in infertile soil, a result which agreed with expectations derived from the physiological trade-off underpinning leaf economic theory. CWM trait–environment relationships were unreliable estimates of how traits affected survival, and should only be used in predictive models when there is empirical support for an evolutionary trade-off that affects vital rates.

Keywords

Community assembly, environmental filtering, flowering phenology, functional traits, plant demography, soil C : N ratio, species interactions, specific leaf area, specific root length.

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INTRODUCTION

The search for phenotypic traits that explain species interactions and compositional turnover along environmental gradients is a major research priority because quantifying the adaptive value of traits will increase the generality of our understanding of species coexistence and responses to global change (HilleRisLambers *et al.* 2012; Adler *et al.* 2013; Kraft *et al.* 2015b). Functional traits are heritable properties that influence organism fitness, but their effect on fitness will depend on the environmental context because variation in traits is underpinned by evolutionary trade-offs (Grime 2001). There are two common approaches for quantifying the fitness of a phenotype. The ‘likelihood’ approach assesses the correlation between community-weighted mean (CWM) traits (average traits weighted by species abundances) and environmental gradients (Ackerly 2003; Shipley *et al.* 2006). The ‘vital rates’ approach models fitness components, such as survival, growth rate and reproduction, directly as functions of trait × environment interactions, because the effect of traits on fitness should depend on the environment (Laughlin & Messier 2015).

The likelihood approach assumes that average trait values in a community are biased towards the optimum trait value for that environment because they are the most frequent trait value in the community. Several trait-based models

(e.g. CATS, TraitSpace, fourth corner and RLQ analyses, Trait Driver Theory) rely on central tendencies of traits at the community level, in some form or another, for understanding the importance of traits in community assembly (Shipley *et al.* 2011; Laughlin *et al.* 2012; Dray *et al.* 2014; Enquist *et al.* 2015; Warton *et al.* 2015). If a sample of CWM traits is significantly correlated with an environmental gradient, then the logical interpretation of this pattern is that the trait has adaptive value along that gradient (Ackerly 2003). If a trait value is more common (i.e. statistically likely) in one environment than another, then species that possess this trait value should exhibit high fitness in that environment (Fig. 1a).

Observed shifts in mean trait values along environmental gradients are interpreted as reflections of physiological trade-offs that drive environmental filtering of regional species pools (Cornwell & Ackerly 2009; Shipley *et al.* 2011; Enquist *et al.* 2015). Examples abound where CWM traits vary predictably along gradients of temperature, precipitation, soil fertility and disturbance (Cornwell & Ackerly 2009; Sonnier *et al.* 2010; Fortunel *et al.* 2014; Jager *et al.* 2015; Ames *et al.* 2016). These relationships can be useful when the aim is to predict the distribution of species and traits across broad spatial scales (Asner *et al.* 2017). However, CWM trait–environment correlations can only be used to explain the value of the trait for fitness when fitness components (i.e. demographic rates) are driven by trait × environment interactions (Fig. 1b, and

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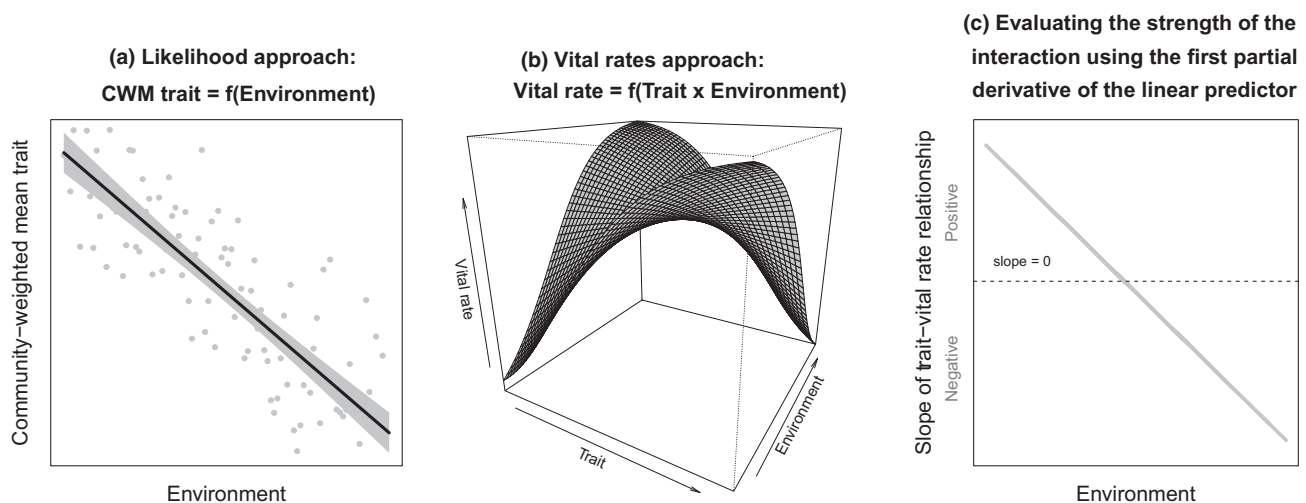


Figure 1 (a) The ‘likelihood’ approach assesses the correlation between community-weighted mean (CWM) traits and environmental gradients. (b) The ‘vital rates’ approach models fitness components, that is, vital rates such as survival and growth rate, directly as functions of species-level trait \times environment interactions. If the likelihood approach is an accurate assessment of the adaptive value of traits, then fitness components must be functions of trait \times environment interactions. For example, (a) if a CWM trait is negatively correlated with an environmental gradient, then (b) high values of that trait will only confer high fitness at the low end of the environmental gradient, leading to an observed interaction between the trait and environment that affects fitness. The presence of a saddle in panel B at intermediate trait values denotes a switch in sign of the slope of the trait–vital rate relationship; see the discussion in Supplementary Information and Fig. S1 for details. (c) The strength of the linear interaction can be assessed by viewing how the sign of the slope of the trait–vital rate relationship, that is, the first partial derivative ($\partial/\partial T$) of the model, changes along the environmental gradient. In this theoretical example, the slope switches from positive to negative along the environmental gradient; note how it is consistent with the sign of the slope in panel A.

see Fig. S1). In other words, the effect of traits on fitness must depend on the environmental context. There are few strong empirical tests of this assumption (Shipley *et al.* 2016). Muscarella & Uriarte (2016) found mixed evidence for the assumption that CWM traits reflect optimum trait values and highlighted the need to analyse demographic data to determine whether CWM trait values in a community reflect the optimum trait value for a given environment.

The likelihood approach is attractive because of its low data requirements and broad applicability to many datasets, but it has four important weaknesses. First and foremost, trait–environment correlations do not measure fitness components directly (Laughlin & Messier 2015). Second, CWM trait–environment relationships could be biased if they are driven by a single dominant species or a large-statured species (Legendre *et al.* 1997; Grime 1998). Small-statured species may be well-adapted to the conditions, but because their low abundances contribute little to the CWM trait value, their fitness is discounted by such an analysis. Third, species composition is dynamic (Adler *et al.* 2006). The dominant trait value in a community at a snapshot in time could be the product of environmental conditions in the past or recent disturbance (Blonder *et al.* 2017), and it could be influenced by dispersal limitation (Ozinga *et al.* 2005). Fourth, the likelihood approach assumes that the fitness function is strictly unimodal, that is, that there is only one optimum trait value for an environment (Muscarella & Uriarte 2016). The complementary coexistence of functionally diverse species (Hooper 1998) and the observation of rugged fitness landscapes (Poelwijk *et al.* 2007) raises doubts about a single optimum trait value. Given these weaknesses, can we assume that CWM

trait–environment correlations are robust proxies for the adaptive value of traits?

Our objective was to conduct a rigorous test of the widespread assumption that CWM trait–environment correlations reflect the adaptive value of functional traits. Fitness, as measured by lifelong reproductive output, is difficult to quantify. Here, we focus on survival, a critical vital rate for perennial herbs (Adler *et al.* 2014). There are four possible outcomes when comparing interpretations of statistical analyses using the likelihood and vital rates approaches (Table S1). When the likelihood approach shows no CWM trait–environment correlations, and trait \times environment interactions do not significantly affect vital rates, then both approaches agree that the trait has no adaptive value (option #1). When there is no CWM trait–environment correlation but the trait \times environment interactions affect vital rates, then the trait may have adaptive value along the gradient, but the CWM traits are being driven by other factors that vary spatially or temporally (option #2). In contrast, when there is a CWM trait–environment correlation but no trait \times environment interaction affecting vital rates, then the trait could be influencing a different fitness component, such as growth or reproduction (Visser *et al.* 2016), or the CWM trait may be generated by a single large or dominant species (option #3). Finally, when the likelihood approach shows strong CWM trait–environment correlations and when trait \times environment interactions significantly affect vital rates (and agree in the direction of the relationships), then both approaches provide evidence that the trait has adaptive value (option #4).

The concordance between the likelihood and vital rates approaches has never been directly tested, possibly because of

the large data requirements that are needed to do so. We have overcome this limitation by analysing a long-term (10-year) dataset from northern Arizona in which we estimated CWM traits and the relationship between traits and survival across 46 perennial plant species in permanent plots along strong orthogonal gradients in soil properties. Specifically, we tested the hypothesis that CWM trait–environment correlations are generated by trait \times environment interactions affecting survival. We found that the effect of traits on survival depended on the environment, but that CWM trait–environment correlations are unreliable estimates of how functional traits influence survival along environmental gradients.

METHODS

Study system and approach

This study was conducted within a 700-km² landscape dominated by ponderosa pine forest near Flagstaff, Arizona (35.19°N, 111.65°W), on the Coconino National Forest between the elevations of 2000–2500 m. The mean annual precipitation of Flagstaff is 565 mm and the mean annual temperature is 7.7 °C. For this analysis, we used 89 permanent 1 – m² chart quadrats mapped between 2003 and 2012 that span a range of soil types developed from basalt, limestone and sandstone parent materials (Laughlin *et al.* 2011).

We tested our hypothesis in two steps: we fit CWM traits as functions of soil gradients and then modelled survival probability using generalised linear mixed models (GLMM) to determine if survival was driven by trait \times soil interactions (Fig. 1). Our primary interest was to estimate the strength of the interactions between each of three traits and the two soil properties to compare with the CWM trait–environment regression models. Our survival models accounted for the many other factors known to influence individual plant survival: plant size, interannual climatic variation and local neighbourhood competition (Lasky *et al.* 2014; Chu & Adler 2015; Kunstler *et al.* 2016).

Demographic data

One of the few ways to determine demographic parameters for perennial plant species is by the long-term mapping of individuals on permanent plots (Clements 1907). This technique allows both the location and basal area of individuals to be tracked through time. We compiled survivorship data for 13 822 individuals representing 46 herbaceous perennial species (10 graminoids and 36 forbs). Species were mapped as either points or polygons depending on growth form. We tracked individuals through time based on their spatial location in the quadrats (Lauenroth & Adler 2008).

For species mapped as points, survivors are classified as any genet identified in year $t + 1$, which is < 5 cm from a conspecific in year t . If in the current year, more than one individual is within the neighbourhood of a ‘parent’ plant, then all individuals inherit that same identity (Lauenroth & Adler 2008). Second, a recruit is defined as a genet in year $t + 1$ which is > 5 cm from any conspecific in year t . For species mapped as polygons, the tracking rules are based on areas of

overlapping polygons, as opposed to distances between points. At time t , a 5-cm buffer is added to all polygons of a given species. At time $t + 1$, if an individual does not overlap with any polygon from the previous year, it is labelled a recruit. Otherwise, it acquires the identity of the individual with which it shares the greatest overlap (Lauenroth & Adler 2008). This allows for individual plants to fragment and coalesce over time. These assumptions and tracking rules are appropriate for the ponderosa pine-bunchgrass ecosystem since most herbaceous species in our quadrats have the potential for clonal growth. A distance of 5 cm was chosen to account for both mapper error and the potential for vegetative growth (Lauenroth & Adler 2008). Analyses of plant demography and coexistence have been shown to be insensitive to this buffer distance (Chu & Adler 2015). Complete details and assumptions of the algorithms are detailed in Lauenroth & Adler (2008).

Forbs and graminoids were mapped differently, so we used the following procedure to convert points and polygons into the same ‘currency’ of abundance, that is, foliar cover. Measurements of basal cover and foliar cover were made on most of these species in an independent dataset in the same region (Moore *et al.* 2006). We developed lifeform-level (i.e. graminoids, forbs and ground-rosette forbs) and species-level regression models to predict foliar cover from basal cover (see Table S2 and Fig. S2 for details). These predictions of foliar cover produced the correct average ratio of 2 : 1 graminoid-to-forb cover (Moore *et al.* 2006).

We used a radius of 15 cm to define the local neighbourhood surrounding each focal plant because the strength of plant–plant interactions was found to decrease rapidly beyond a radius of 10 cm in western U.S. rangelands (Chu & Adler 2015). We used a slightly larger radius than this in order to include more potential competitors, and to limit edge effects, we excluded all individuals within 5 cm of the quadrat border.

Environmental conditions

We analysed a variety of soil properties to select two uncorrelated soil properties that reflect independent edaphic gradients (see Supplementary Information for detailed methods). We selected sand content and soil C : N ratio because they were orthogonal variables that reflect different aspects of the soil environment (Fig. S3). Soil with high sand content was higher in pH and tended to be warmer and drier than soil with low sand content. C : N ratio was orthogonal to sand content, and soil with low C : N ratios has greater available nitrogen.

We computed average annual temperatures and total annual water-years using data obtained from the National Climatic Data Center (www.ncdc.noaa.gov) for the Flagstaff, Arizona region. Gaps in the data were supplemented with local weather stations. Water-years were defined as the total precipitation that fell from October of previous year through September of current year. We compared models to preselect whether to use the current or previous year’s precipitation and temperature. Based on AIC, we chose the current year’s temperature and the previous year’s water-year (hereafter, precipitation) because they were superior predictors of plant survival (Table S3).

Functional traits

We used three functional traits thought to influence plant performance along gradients of soil properties and climatic conditions: specific leaf area (SLA), specific root length (SRL) and flowering phenology (see Supplementary Information for detailed methods). These traits loaded on distinct axes of variation and so reflect different dimensions of plant function in this flora (Laughlin *et al.* 2010). SLA reflects a trade-off between performance and persistence where leaves with high SLA have short lifespans and high rates of gas exchange (Poorter *et al.* 2009). Species with high SLA are thought to exhibit superior performance in soils that are rich in water and mineral nutrients (Jager *et al.* 2015; Maire *et al.* 2015). SRL reflects the foraging potential of the root per unit carbon investment. Species with high SRL are thought to be superior foragers when soil nutrients, especially phosphorus, are limited because they are better able to proliferate into nutrient-rich patches of soil (Laliberté *et al.* 2015). Flowering date reflects phenological differences that may reflect tolerance of water limitation, where early flowering ‘cool-season’ species tolerate cooler conditions and wetter soils, and late-flowering ‘warm-season’ species tolerate warmer conditions and drier soils.

Data analysis

First, we computed quadrat-level CWM trait values, which represent the average value of a given trait within a quadrat weighted by the relative abundance of each species. CWM traits were calculated for each trait in each of the k quadrats as $CWM_k = \sum_{i=1}^S t_i p_{ik}$, where t_i is the mean trait of species i , p_{ik} is the relative foliar cover of species i in plot k , and S is the number of species in the plot. We computed CWM traits for each quadrat in each year, but these average trait values did not change appreciably throughout the study period so we used the average CWM for each quadrat across all years. We first fit multiple regression models that tested for interaction effects between soil sand content and C : N ratio, but no interactions among soil properties were detected ($P > 0.05$). We also tested for nonlinear relationships by including a quadratic predictor variable, but there was no evidence of nonlinear relationships ($P > 0.05$). Therefore, we illustrate the simple linear relationships in bivariate scatterplots.

Second, survival was modelled using a logit link function within a GLMM of the general form:

$$\begin{aligned} \text{logit}(\text{survival}) = & \alpha + \gamma_{sp} + \text{size}\beta_{sp} + \delta_{quad} + \tau_{yr} + \text{size}\beta_1 + \\ & \text{trait}\beta_2 + \text{CNratio}\beta_3 + \text{sand}\beta_4 + \text{precip}\beta_5 \\ & + \text{temp}\beta_6 + \text{intraCover}\beta_7 + \text{interCover}\beta_8 \\ & + \text{trait} \times \text{CNratio}\beta_9 + \text{trait} \times \text{sand}\beta_{10} \\ & + \text{trait} \times \text{precip}\beta_{11} + \text{trait} \times \text{temp}\beta_{12} \\ & + \text{trait} \times \text{intraCover}\beta_{13} + \text{trait} \\ & \times \text{interCover}\beta_{14} \end{aligned}$$

To maintain model tractability, each model tested the effects of a single trait and its interactions; we did not test for higher-ordered multi-trait interactions. This model included

three random effects, eight main effects (not including the global intercept α) and six interactions. We modelled species as a random intercept (γ_{sp}) to account for species-level differences in survival that were unrelated to the traits. These random species effects were allowed to exhibit random slopes (β_{sp}) with respect to plant size because the effect of size on survival can differ among species (Fig. S4). We modelled quadrats as random intercepts (δ_{quad}) to account for spatial autocorrelation (Fig. S5), and we modelled years as random intercepts (τ_{yr}) to account for annual variation in survival unrelated to interannual climate (Fig. S6).

Two conditions had to be satisfied in order for us to consider a trait \times environment interaction to be ‘strong’. First, the interaction terms in the GLMM had to be statistically significant ($\alpha = 0.05$). Second, the slope of the relationship between the trait and logit survival must switch signs over the length of the environmental gradient (Fig. 1c). This was computed as the first partial derivative of the fitted model (see Supplementary Information). We consider statistically significant interactions as ‘weak’ if the slope of the trait–logit survival relationship does not switch signs along the environmental gradient, or as ‘strong’ if the slope does switch signs. This is important because ‘strong’ interactions indicate that there is a change in the rank order of fitness across the gradient, which is required for there to be a predictable change in CWM trait values across the gradient (Fig. 1).

We simultaneously accounted for other factors known to affect survival. We used foliar plant cover of the individual to account for plant size. The previous year’s precipitation and the current year’s temperature and their interactions with the trait of the focal plant were used to account for climatic effects (Table S3). We partitioned the effects of local neighbourhood competition into four different effects. First, the cover of conspecifics accounts for the main effect of intraspecific competition on focal plant survival. Second, the interaction between conspecific cover and the trait of the focal plant accounts for how the trait mediates the effect of intraspecific competition on the survival of the focal plant. Third, the cover of heterospecifics accounts for the main effect of interspecific competition on focal plant survival, and fourth, we account for the interaction between heterospecific cover and the trait of the focal plant (Kunstler *et al.* 2016).

We used the ‘glmer’ function in the ‘lme4’ package in R to fit these models (Bates *et al.* 2015). We computed the marginal R^2 (hereafter, R^2_m , the proportion of variance explained by the fixed effects) and the conditional R^2 (hereafter, R^2_c , the proportion of variance explained by both fixed and random effects) using the ‘piecewiseSEM’ package in R (Lefcheck 2015).

RESULTS

Comparison of likelihood and vital rates approaches

CWM-specific leaf area (SLA) was not related to either sand content ($R^2 < 0.01$, Fig. 2a) or soil C : N ratio ($R^2 = 0.01$, Fig. 2d). In the survival analysis, the interaction between SLA and sand content was not significant ($P = 0.11$, Table 1, Fig. 2b,c), so the vital rates approach agreed with the likelihood approach with respect to SLA and sand content

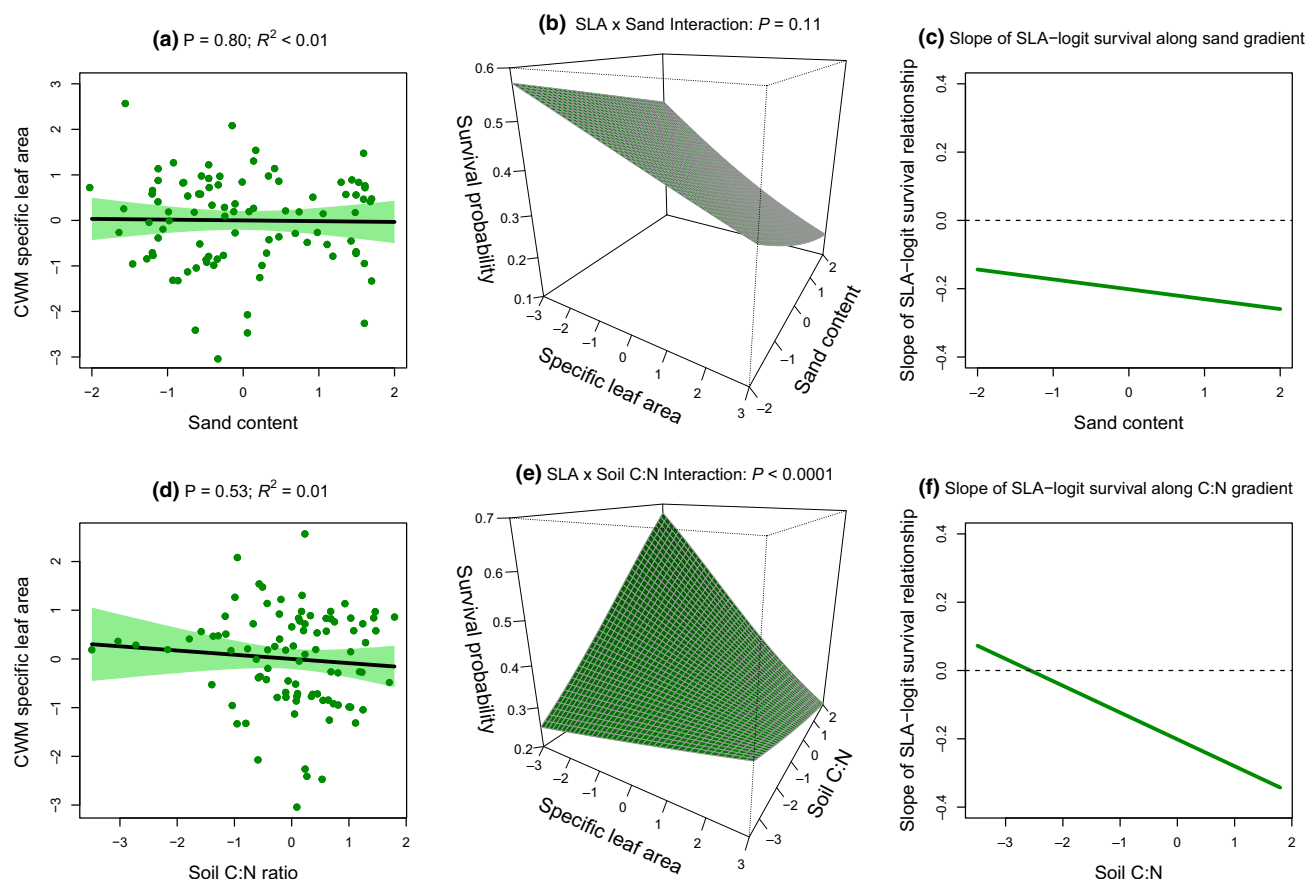


Figure 2 Comparison of likelihood and vital rates approaches for examining the adaptive value of specific leaf area (SLA) along two soil property gradients. The first column illustrates the results of the likelihood approach, where community-weighted mean (CWM) SLA was regressed on each soil property across the 89 quadrats (a,d). The second column illustrates the results of the vital rates approach, where the GLMM fitted predictions of survival probability (curved surfaces) illustrate the interactions between the trait and each soil property (b,e). The third column illustrates how the slope of the trait–logit survival relationship changes along each soil property gradient, and the dotted line indicates a slope of zero (c,f). All variables have been scaled to unit variance.

Table 1 GLMM standardised coefficients and their significance, and model fit statistics for each of the three trait-based models

Term	Specific leaf area		Specific root length		Flowering date	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Intercept	−0.472	0.0640	−0.600	0.0206	−0.513	0.0404
Trait	−0.202	0.2015	−0.213	0.1092	0.066	0.6857
Precipitation (previous year)	−0.014	0.9430	−0.006	0.9734	−0.001	0.9956
Temperature (current year)	0.013	0.9459	0.007	0.9713	−0.011	0.9540
Sand content	−0.195	< 0.0001	−0.220	< 0.0001	−0.184	< 0.0001
Soil C : N ratio	0.097	0.0351	0.123	0.0101	0.131	0.0067
Local intraspecific cover	−0.502	< 0.0001	−0.469	< 0.0001	−0.458	< 0.0001
Local interspecific cover	−0.107	< 0.0001	−0.104	< 0.0001	−0.100	< 0.0001
Focal plant size	0.777	< 0.0001	0.813	< 0.0001	0.816	< 0.0001
Trait × Precipitation	0.040	0.0031	−0.095	< 0.0001	−0.087	< 0.0001
Trait × Temperature	0.048	0.0009	0.056	< 0.0001	0.114	< 0.0001
Trait × Sand content	−0.029	0.1381	0.086	< 0.0001	0.085	< 0.0001
Trait × Soil C : N ratio	−0.079	< 0.0001	−0.036	0.0586	0.015	0.3698
Trait × Intraspecific cover	0.146	< 0.0001	−0.037	0.0516	0.068	0.0001
Trait × Interspecific cover	−0.033	0.0208	−0.068	0.0001	−0.025	0.0974
Model fit statistics						
R^2_{marginal}	0.166		0.164		0.161	
$R^2_{\text{conditional}}$	0.428		0.422		0.423	

Significant terms are in bold.

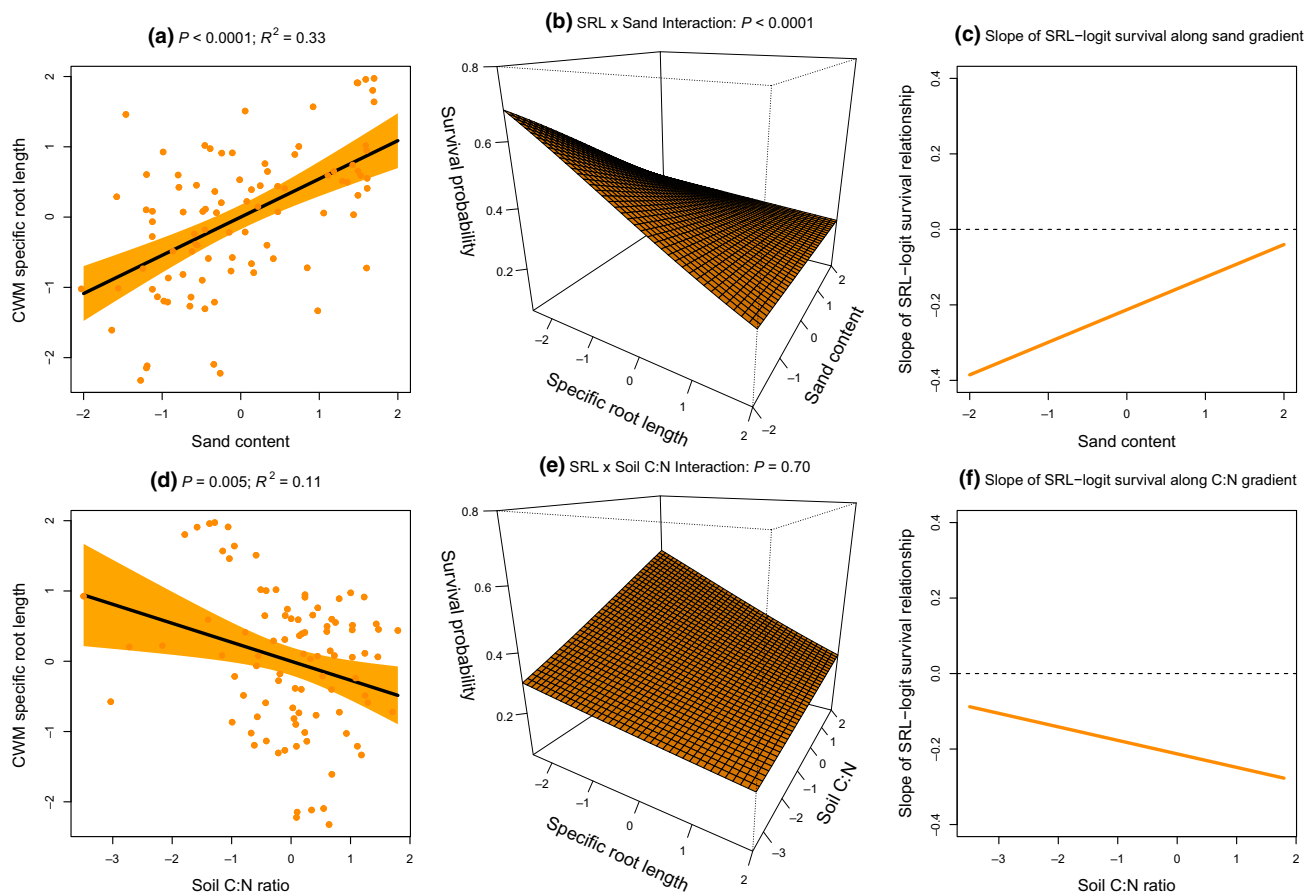


Figure 3 Comparison of likelihood and vital rates approaches for examining the adaptive value of specific root length (SRL) along two soil property gradients. The first column illustrates the results of the likelihood approach, where community-weighted mean (CWM) SRL was regressed on each soil property across the 89 quadrats (a,d). The second column illustrates the results of the vital rates approach, where the GLMM-fitted predictions of survival probability (curved surfaces) illustrate the interactions between the trait and each soil property (b,e). The third column illustrates how the slope of the trait–logit survival relationship changes along each soil property gradient, and the dotted line indicates a slope of zero (c,f). All variables have been scaled to unit variance.

(outcome #1 in Table S1). However, there was a significant interaction between SLA and soil C : N ratio (Fig. 2e, Table 1). In high C : N ratio soil, survival was highest for species with low SLA and lowest for species with high SLA. The slope of the relationship between SLA and logit survival switched from positive to negative along the soil C : N ratio gradient (Fig. 2f); therefore, the vital rates and likelihood approaches were inconsistent with respect to the effect of SLA on survival along a soil C : N ratio gradient (outcome #2 in Table S1).

CWM-specific root length (SRL) was positively related to sand content ($R^2 = 0.33$, Fig. 3a) and negatively related to soil C : N ratio ($R^2 = 0.11$, Fig. 3d). In the survival analysis, there was a significant interaction between SRL and soil sand content, such that survival was highest for species with low SRL in soil with low sand content (Fig. 3b, Table 1). However, the slope of the relationship between SRL and logit survival did not switch from negative to positive across the sand content gradient, indicating a relatively weak interaction (Fig. 3c); therefore, the interpretations of the likelihood and vital rates results were in disagreement (outcome #3 in Table S1). The interaction between SRL and soil C : N ratio was not

significant (Fig. 3e, Table 1), also conflicting with the results of the likelihood approach (outcome #3 in Table S1).

CWM flowering date was positively related to sand content ($R^2 = 0.21$, Fig. 4a) and negatively related to soil C : N ratio ($R^2 = 0.10$, Fig. 4d). The survival analysis showed a significant interaction between flowering date and sand content, such that survival was higher for species with later flowering dates in sandy soil and lower for species with early flowering dates in sandy soil (Fig. 4b, Table 1). The slope of the relationship between flowering date and logit survival switched from negative to positive along the sand content gradient (Fig. 4c). Therefore, with respect to flowering date and sand content, the likelihood and vital rates approaches were in agreement (outcome #4 in Table S1). However, the interaction between flowering date and soil C : N ratio was not significant (Figs. 4e,f, Table 1), conflicting with the results of the likelihood approach (outcome #3 in Table S1).

Other factors affecting survival

No trait exhibited significant main effects on survival (Table 1, Fig. 5a,d,g). In other words, the effects of traits on

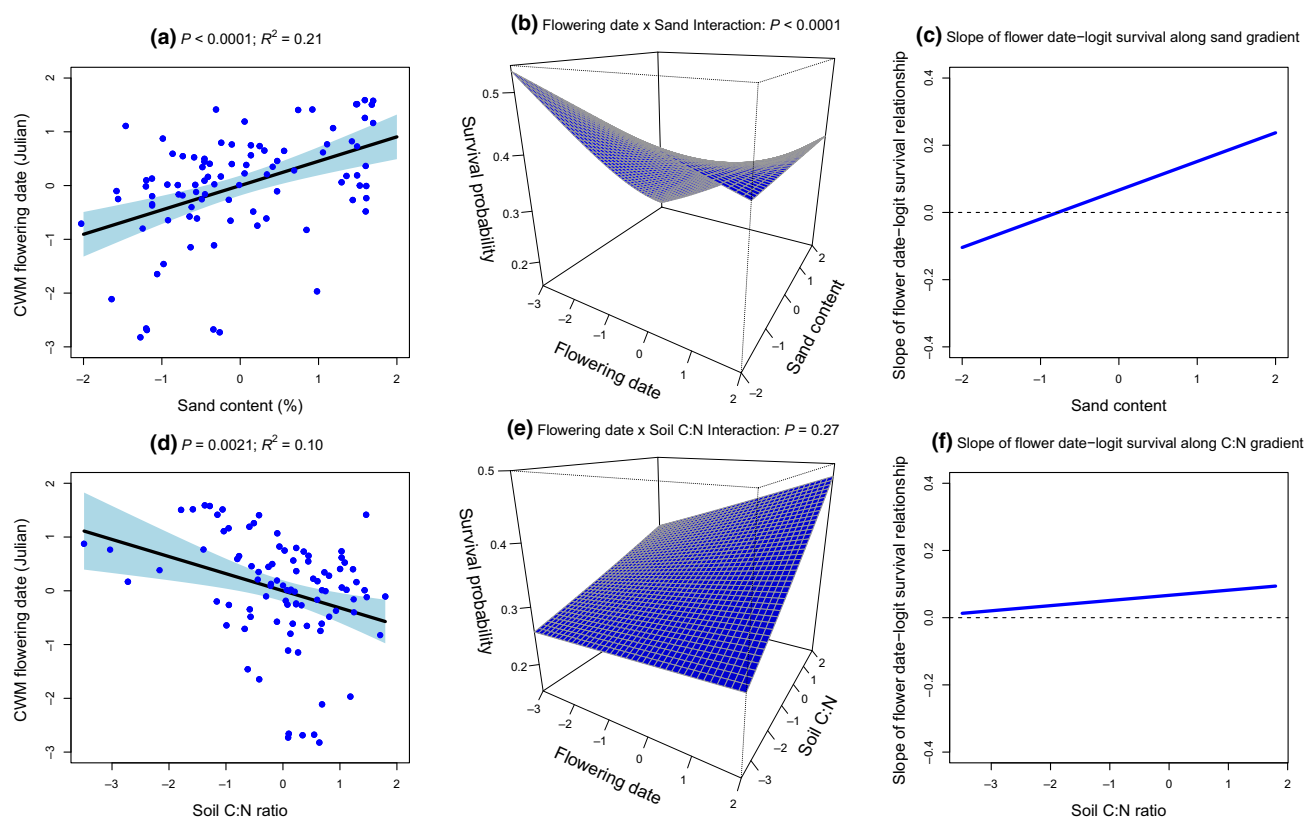


Figure 4 Comparison of likelihood and vital rates approaches for examining the adaptive value of flowering date along two soil property gradients. The first column illustrates the results of the likelihood approach, where community-weighted mean (CWM) flowering date was regressed on each soil property across the 89 quadrats (a,d). The second column illustrates the results of the vital rates approach, where the GLMM fitted predictions of survival probability (curved surfaces) illustrate the interactions between the trait and each soil property (b,e). The third column illustrates how the slope of the trait–logit survival relationship changes along each soil property gradient, and the dotted line indicates a slope of zero (c,f). All variables have been scaled to unit variance.

survival always depended on the abiotic and biotic context. SLA of the focal plant interacted with intraspecific cover, such that species with low SLA had higher survival where neighbourhood competition with conspecifics was low and species with high SLA exhibited higher survival where cover of conspecifics was high (Fig. 5b). SLA weakly interacted with temperature and precipitation, such that species with low SLA had the highest survival in cold and dry years (Fig. 5c,d). SRL did not interact with intraspecific cover (Fig. 5f). SRL weakly interacted with temperature and precipitation such that low SRL was associated with higher survival at low temperatures (Fig. 5g) and high precipitation in the previous year (Fig. 5h). Flowering date interacted weakly with intraspecific cover (Fig. 5j), but interacted strongly with interannual climate. Survival was highest for species with late-flowering dates in hot years with dry previous years, whereas survival was highest for species with early-flowering dates in cool years with wet previous years (Fig. 5k,l).

Among all the trait-independent main effects, focal plant size was the most important predictor of survival (Table 1). Large plants exhibited significantly higher survival probabilities (Fig. S7a), and this size dependence differed among species (Fig. S4). Intraspecific and interspecific cover of the local neighbourhood surrounding the focal plants were each

negatively related to survival, but intraspecific cover exhibited the stronger effect (Fig. S7b,c). Neither precipitation in the previous year nor temperature of the current year was significantly related to survival (Fig. S7d,e). Sand content was negatively related to survival, and soil C : N content was positively related to survival (Fig. S7f,g).

The fixed effects in the survival models explained approximately 16% of total variation in survival ($R^2_m = 0.16$), leaving approximately 26% of the variation accounted for by the random effects ($R^2_c = 0.42$). Random species effects (standard deviation [SD] for the random intercept = 0.97) accounted for more variation than random quadrat effects (SD for the random intercept = 0.12) or random year effects (SD for the random intercept = 0.36) (Figs. S4, S5, S6).

DISCUSSION

By synthesising data on long-term demographic rates and functional traits across a strong gradient in soil properties, we conducted a rigorous test of the assumption that CWM trait–environment correlations are accurate reflections of the adaptive value of traits. After accounting for focal plant size, climatic effects and local neighbourhood competitive interactions (Chu & Adler 2015; Kraft *et al.* 2015a), we have shown

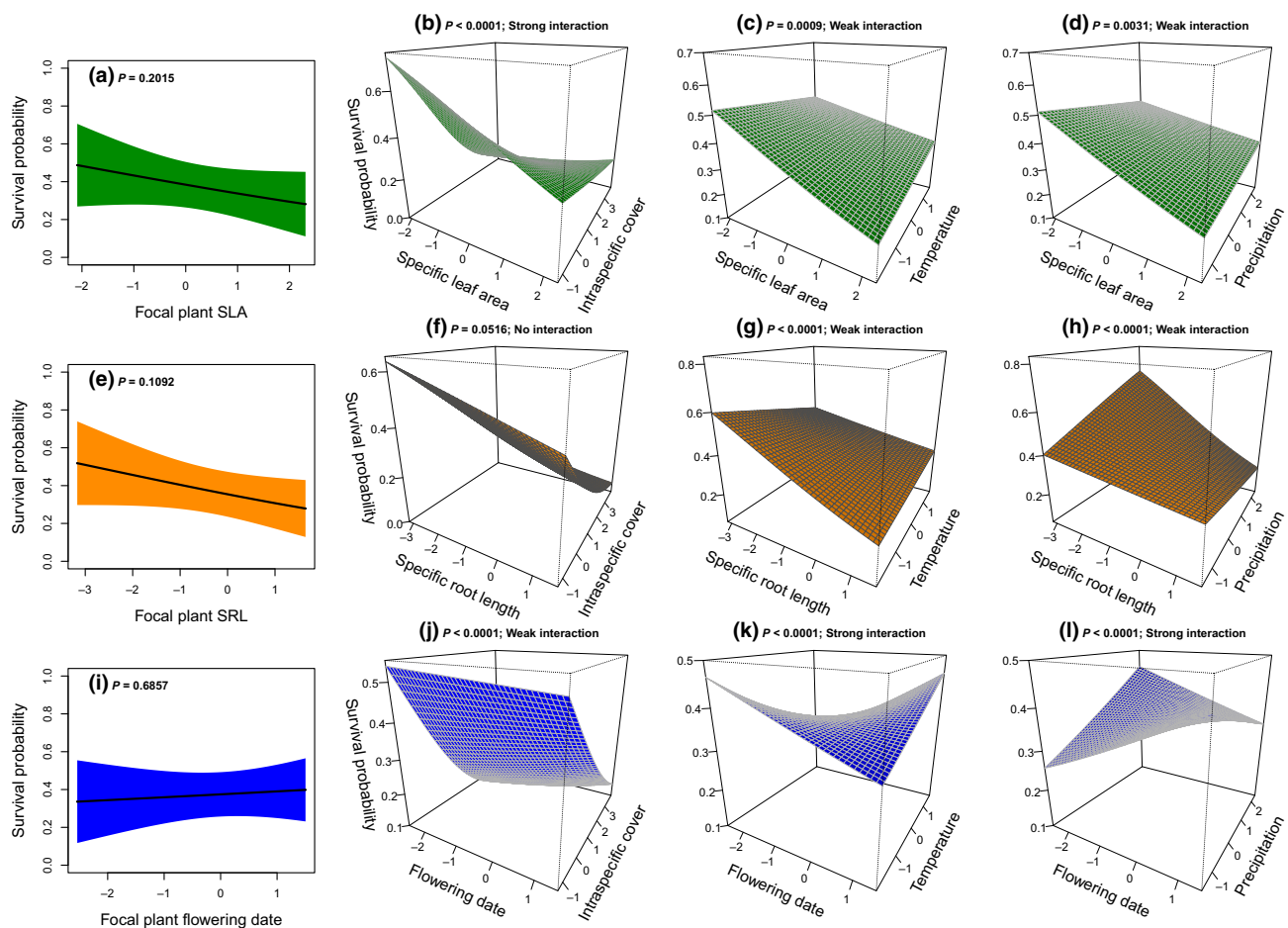


Figure 5 Main effects of the focal plant trait (first column on left) and trait \times environment interaction effects (three columns on right) estimated in the GLMMs. For the nonsignificant main effects, lines represent model fitted predictions and shading represents 95% confidence intervals. For the interaction effects, curved surfaces represent the GLMM predictions as functions of the interactions between each trait and environmental variable. The P -values indicate the significance of the interaction terms; ‘weak’ interactions did not exhibit trait–logit survival relationships that switched signs along the length of the environmental gradient, whereas ‘strong’ interactions exhibited trait–logit survival relationships that switched signs. All variables have been scaled to unit variance.

that the effects of traits on survival depends on the environmental conditions. However, we observed inconsistencies between the likelihood and vital rates approaches (Laughlin & Messier 2015), contradicting the hypothesis that CWM trait–environment correlations are generated by trait \times environment interactions affecting survival. If the likelihood and vital rates approaches were consistent, then we should have only observed outcomes #1 and #4 as listed in Table S1, but we observed all four possible outcomes. We conclude that CWM trait–environment correlations are unreliable estimates of how traits mediate survival probabilities across environmental gradients. CWM traits are often used to estimate optimum trait values, but processes such as environmental change, disturbance and dispersal limitation can shift CWM traits from an optimum value. Linking vital rates to trait \times environment interactions will advance our understanding of trait-based habitat filtering and will improve our ability to accurately predict how species and communities respond to environmental gradients.

No trait exhibited independent main effects on survival because the adaptive value of traits depended on the

environmental context. For example, variation in SLA is underpinned by a physiological trade-off between metabolic rate and leaf longevity (Poorter *et al.* 2009). The vital rates analysis supported the prediction from leaf economics theory that conservative phenotypes would have high survival in resource-poor environments (Maire *et al.* 2015): species with low SLA had higher survival in high C : N ratio soil and species with high SLA had higher survival in low C : N ratio soil (Fig. 2f). However, the likelihood approach failed to detect the positive effect of low SLA on survival in high C : N ratio soil because there was no correlation between CWM SLA and soil C : N ratio. This suggests that other unmeasured factors, such as grazing or other disturbances (Strahan *et al.* 2015) or dispersal limitation (Ozinga *et al.* 2005), have shifted the CWM trait values in each plot away from any optimal value (Table S1). In other words, a CWM trait–environment correlation is the result of multiple processes, and we urge caution when interpreting these correlations as evidence for the adaptive value of a trait in the absence of a known physiological trade-off that can explain the correlation.

The predictive power of the survival models was limited (marginal $R^2 < 0.20$), suggesting that other drivers of survival were missing from the models. The empirical interaction effects were rarely as strong as theoretical expectations (Fig. 1), and many significant interaction terms were not considered to be 'strong' because the slope of the trait and logit survival relationship did not switch signs along the length of the environmental gradient. The predictive power of these models could be low because survival is influenced by complex trait combinations expressed at the level of the whole phenotype. For example, low SRL may confer higher survival in low sand content soil, but high SRL leads to low survival probabilities across the entire sand content gradient (Fig. 3); however, species with high SRL might exhibit higher probabilities of survival in sandy soil if they also exhibit later flowering times (Fig. 4). Explicit tests of the effects of multiple trait combinations via higher-ordered trait \times trait \times environment interactions are an important next step towards understanding the effects of whole-organism phenotypes on fitness; however, expanding models to higher-ordered interactions will exponentially increase the number of model parameters and will require sufficient data for accurate estimation.

Discrepancies between the likelihood and vital rates may occur if a trait is influencing another fitness component other than survival. There was surprisingly no detectable interaction between SRL and soil C : N ratio despite the CWM trait–environment correlation between these two variables. Similarly, there was no detectable flowering date \times soil C : N ratio interaction despite the CWM trait–environment correlation between these two variables. These discrepancies could possibly be explained if SRL and flowering date were influencing growth rates or reproduction (Table S1). For example, SRL is positively related to relative growth rate (Comas & Eissenstat 2004; Kramer-Walter *et al.* 2016), and phenological differences among species could affect reproductive success in changing climates (Galen & Stanton 1991; Cleland *et al.* 2007).

Temporal dynamics in these communities were driven by two main factors: local competitive interactions and interannual climatic variability. Intraspecific competitive effects on focal plant survival were much stronger than interspecific competitive effects on survival because survival probability approached zero in the presence of high abundances of the same species (Fig. S7b). The traits of the focal plant moderated the effects of competition on survival. For example, herbaceous plant species with high SLA had higher survival when competition with conspecifics was high, whereas species with low SLA had higher survival in the absence of competition. This suggests that productive phenotypes are winners when competition with conspecifics is most fierce.

Interannual variation in temperature and precipitation also influenced plant survival, but phenological differences moderated these survival responses. Specifically, species with later flowering dates, which tend to be affiliated with a warm-season strategy or the C_4 photosynthetic pathway (Laughlin *et al.* 2010), had higher survival than species with early-flowering dates following drought years. Late-flowering species had higher survival in hot years and early-flowering species had higher survival in cool years, suggesting that quantitative traits can be used to forecast how species and communities will

respond to interannual climatic variation and changing climate (Anderegg *et al.* 2016). Interannual climatic variation has been shown to have a stabilising effect on species coexistence (Adler *et al.* 2006), and phenotypic traits provide a generalisable predictor of how species respond to yearly climatic variation.

It could be argued that CWM trait–environment relationships are better metrics of adaptation than demographic rates because they are the integrated sum of many vital rates over a longer period of time. Moreover, CWM traits implicitly include the effects of species interactions and other unmeasured processes. In contrast, survival probability and other fitness components may be sensitive to factors such as disturbance that vary stochastically over time and space. For this and other practical reasons, the likelihood approach will likely remain a useful tool for generating predictions about species and community distributions in an era of global change. CWM traits also have clearer effects on ecosystem processes. However, if we assume that a CWM trait–environment relationship reflects the adaptive value of a trait in the absence of a known physiological trade-off, this could lead to incorrect predictions of responses for other species in different ecosystems. In other words, correlative patterns will most successfully be used to make general predictions if the correlation is underpinned by an evolutionary trade-off driven by a physiological mechanism that influences vital rates.

Community-weighted mean traits are easy to compute but difficult to interpret. We hope that our results motivate others to undertake the challenging task of quantifying how the effect of traits on individual and population-level fitness depends on the environmental context. A phenotype may be dominant because of higher survival, growth and/or reproduction (Adler *et al.* 2014), so if a trait affects survival differently than it affects growth rates or reproduction (Visser *et al.* 2016), then effects on lifelong fitness are obscured. Future work that estimates the effects of multiple trait combinations on total fitness, by integrating all vital rates to estimate population-level growth rates (λ) using Integral Projection Models, may provide much-needed insight into how phenotypes affect fitness across environmental gradients.

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AUTHOR CONTRIBUTIONS

DCL wrote the paper; DCL, RTS and PBA analysed the data; DCL, RTS and MMM collected the data; and RTS, PBA and MMM edited the paper.

DATA ACCESSIBILITY STATEMENT

The data and R code are available online at Northern Arizona University Cline Library's Open Knowledge repository (<http://openknowledge.nau.edu/5232/>).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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